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Temporal changes in vegetation of a virgin beech woodland remnant: stand-scale stability with intensive fine-scale dynamics governed by stand dynamic events

Tibor Standovár[1], Soma Horváth[1], Réka Aszalós[2]

1 *Department of Plant Systematics, Ecology and Theoretical Biology, Institute of Biology, L. Eötvös University, Pázmány P. sétány 1/c, H-1117 Budapest, Hungary* **2** *MTA Centre for Ecological Research, Institute of Ecology and Botany, Alkotmány u. 2-4., H-2163 Vácrátót, Hungary*

Corresponding author: *Tibor Standovár* (standy@caesar.elte.hu)

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Abstract

The aim of this resurvey study is to check if herbaceous vegetation on the forest floor exhibits overall stability at the stand-scale in spite of intensive dynamics at the scale of individual plots and stand dynamic events (driven by natural fine scale canopy gap dynamics). In 1996, we sampled a 1.5 ha patch using 0.25 m^2 plots placed along a 5 m × 5 m grid in the best remnant of central European montane beech woods in Hungary. All species in the herbaceous layer and their cover estimates were recorded. Five patches representing different stand developmental situations (SDS) were selected for resurvey. In 2013, 306 plots were resurveyed by using blocks of four 0.25 m^2 plots to test the effects of imperfect relocation.

We found very intensive fine-scale dynamics in the herbaceous layer with high species turnover and sharp changes in ground layer cover at the local-scale (< 1 m^2). A decrease in species richness and herbaceous layer cover, as well as high species turnover, characterized the closing gaps. Colonization events and increasing species richness and herbaceous layer cover prevailed in the two newly created gaps. A pronounced decrease in the total cover, but low species turnover and survival of the majority of the closed forest specialists was detected by the resurvey at the stand-scale. The test aiming at assessing the effect of relocation showed a higher time effect than the effect of imprecise relocation.

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The very intensive fine-scale dynamics of the studied beech forest are profoundly determined by natural stand dynamics. Extinction and colonisation episodes even out at the stand-scale, implying an overall compositional stability of the herbaceous vegetation at the given spatial and temporal scale. We argue that fine-scale gap dynamics, driven by natural processes or applied as a management method, can warrant the survival of many closed forest specialist species in the long-run.

Nomenclature: Flora Europaea (Tutin et al. 2010) for vascular plants; Soó 1968–1980 for syntaxa

Keywords

Deciduous forest, temperate forest, resurvey, forest reserve, forest developmental stage, *Fagus sylvatica*, ancient forest herbs

Introduction

The significance of the herbaceous layer in forest biodiversity and ecosystem functioning has been widely appreciated (Whigham 2004, Gilliam 2014), generating an interest in its dynamics. During the last decade, remarkable changes in the herbaceous layer have been shown by several studies (e.g. reviewed in Verheyen et al. 2012). Resurvey studies investigated the understorey to detect potential long-term changes and to assess the role of different environmental variables as driving forces in deciduous forests. The observed changes were attributed to different background causes, such as combined effect of temperature increase and canopy opening (De Frenne et al. 2013, 2015), abandonment of former forest management practices (Hédl et al. 2010, Heinrichs et al. 2014), lack of disturbance (Brewer 1980, Taverna et al. 2005), deer herbivory (Rooney and Dress 1997, Taverna et al. 2005, Wiegmann and Waller 2006), increased soil acidity (Falkengren-Grerup and Tyler 1991, Durak 2010, Šebesta et al. 2011), nitrogen deposition (Verheyen et al. 2012) and often the intermingled influence of several factors (Heinrichs et al. 2014, Vanhellemont et al. 2014, Bernhardt-Römermann et al. 2015, Naaf and Kolk 2016). The majority of the observed changes in the herbaceous layer show an explicit trend, as a consequence of direct or indirect anthropogenic effects. A marked successional shift towards species-poorer herbaceous layer communities was detected as a result of abandonment of former management practices (Baeten et al. 2010, Hédl et al. 2010), lack of disturbance (Brewer 1980) and herbivory (Rooney and Dress 1997). A loss of rarer native plants (Hédl 2004) and the homogenization of the herbaceous layer was detected, and was attributed to high browsing pressure by deer herbivory (Wiegmann and Waller 2006), acidification (Durak 2010) and light deficit (Davison and Forman 1982, Heinrichs et al. 2014).

Fine-scale herbaceous layer dynamics is also often linked to stand-scale dynamics. Gap formation significantly increases solar radiation and soil moisture (Collins et al. 1985, Moore and Vankat 1986, Gálhidy et al. 2006) leading to intensive alteration of composition and cover of the herbaceous layer (Gálhidy et al. 2006,

Kelemen et al. 2012) in large (Degen et al. 2005) and small gaps (Mountford et al. 2006). Stand dynamic events were matched with certain vegetation changes in different Slovakian primeval forests (Ujházy et al. 2005, 2007, Martináková and Martinák 2012). The herbaceous layer was best developed at the beginning of the decaying stage, and its cover sharply decreased when the tree seedlings and saplings overgrew them at the end of the decaying stage and in the growing stage. Herbaceous layer vegetation change can have a cyclic pattern, especially in forest stands that do not experience the strong successional effect of abandonment or other marked environmental change. Ujházy et al. (2007) detected low species turnover and cyclic changes in a Slovakian primeval forest at the stand-scale. Changing abundance or dominance of herb species characterized the cyclic changes, which was interpreted as internal community dynamics (Van Der Maarel 1996, Ujházy et al. 2005). Carøe et al. (2000) could not detect a successional trend either, only changes in species abundance in a managed Danish beech forest. Neither could Martináková and Martinák (2012) in a Slovakian natural fir-beech forest; however, the time interval was short in both investigations.

These short- and long-term changes in the herbaceous layer are most often detected by resurveys of phytosociological relevés or smaller quadrats after a few years (Ujházy et al. 2007, Martináková and Martinák 2012), one or a few decades (Davison and Forman 1982, Taverna et al. 2005, Łysik 2008, 2009, Vanhellemont et al. 2014) or even after a half-century interval (Brewer 1980, Hédl 2004, Durak 2010, 2012, Hédl et al. 2010, Šebesta et al. 2011). In some cases the relocation can be precise, when the time span is short or permanent corner markers were used, but more often former plots are relocated only approximately. The error resulting from relocation uncertainty can be high, especially in the case of small plots (Kopecký and Macek 2015). However, if relocation is done carefully, the resurvey can be robust to localization uncertainty, and can provide evidence of long-term changes in the herbaceous layer (Chytrý et al. 2014, Kopecký and Macek 2015). Ross et al. (2010) also demonstrated that if temporal change in the vegetation is greater than recent spatial heterogeneity, results of the resurveys can be interpreted with some confidence.

In our study, we were especially interested in the dynamics of the herbaceous layer at multiple spatial scales in relation to simple stand dynamic events, such as the opening and closure of smaller and larger gaps of a primeval beech forest remnant in Hungary. The exact location of the original sampling plots surveyed in 1996 was unknown, but the sampling plots could be relocated with 1 m accuracy after 17 years.

We hypothesized that in this virgin woodland remnant: 1) fine-scale changes in the herbaceous layer are evened out at the stand-scale, where no significant changes can be detected in the species pool (low species turnover) and total cover of the herbaceous layer at this temporal and spatial scale; 2) fine-scale changes in the herbaceous layer are governed by dynamic events in the tree canopy, such as opening and closing of the canopy gaps; 3) small gap stand dynamics warrant the survival of closed forest specialist herbs at the stand-scale.

Methods

Study area

The study was carried out in Kékes Forest Reserve (63 ha), which is one of last and best remnant of central European montane beech woods in Hungary. Kékes is the highest point in Hungary (1014 m) and is situated in the Mátra Mountains, northern Hungary. The climate is relatively continental. Mean annual precipitation is around 840 mm, of which 480 mm fall during the growing season. Mean annual temperature is 5.7°C, with cold winter (-4.7°C in January) and mild summer temperatures (15.5°C in July). The bedrock is andesite and andesitic tuff. The topography is extremely steep; scree slopes are characteristic. The shallow brown forest soils are mainly covered by montane beech forest (*Aconito-Fagetum* Soó (1930) 1960). Mixed maple-ash-lime forest (*Phyllitidi-Aceretum* Moor, 1952 *subcarpaticum* (Dostál 1933) Soó 1957) occurs in the most humid and rocky patches of the reserve on ranker type soils (Kovács 1968, Soó 1980).

According to historical records (Czájlik 2009) the area has never been used for timber production. As a result, most parts of the reserve show the characteristic fine-scale mosaic of forest developmental stages – sensu Korpeľ (1995) – of central European montane beech forests. For the purpose of the original survey we selected a roughly 1.5 ha plot in the reserve that contained a closed old beech stand, a small gap in the beech stand, and a larger collapse on a rockier site.

Data collection

In 1996, vegetation of the herbaceous layer was systematically sampled in a 120 m × 120 m patch (approximately 1.5 ha), which was divided into 16 30 m × 30 m squares with wooden sticks as field marks in the four corners. On the 120 m × 120 m patch a grid with 5 m intervals was laid out. Altogether 576 plots with 0.25 m^2 were set out on the grid (see Suppl. material 1). All grasses, sedges, herbs as well as trees and shrubs lower than 0.5 m in height were included in the sample (Gilliam 2007). Total vegetation cover and cover for each vascular plant species were estimated in percentage.

To make future assessment of stand dynamics possible, in 1997 a tree stand position map (each tree individual recorded by X and Y coordinates) was created for the 1.5 ha plot (see Suppl. material 2). The map was also used to assist the approximate relocation of the 0.25 m^2 plots, as they were not permanently marked in 1996. Partial resurvey of the herbaceous vegetation was carried out in 2013. The aim was to compare 17-year vegetation change within and between the patches with different histories of stand dynamics. To select the appropriate patches, we used the stand position map and a series of archive aerial photographs to detect the location and time of certain events in stand development. Using the same methods, we resampled 306 plots representing five different stand developmental situations (see Suppl. materials 1 and 2). However, because of the lack of permanent marking of the original sampling locations, reloca-

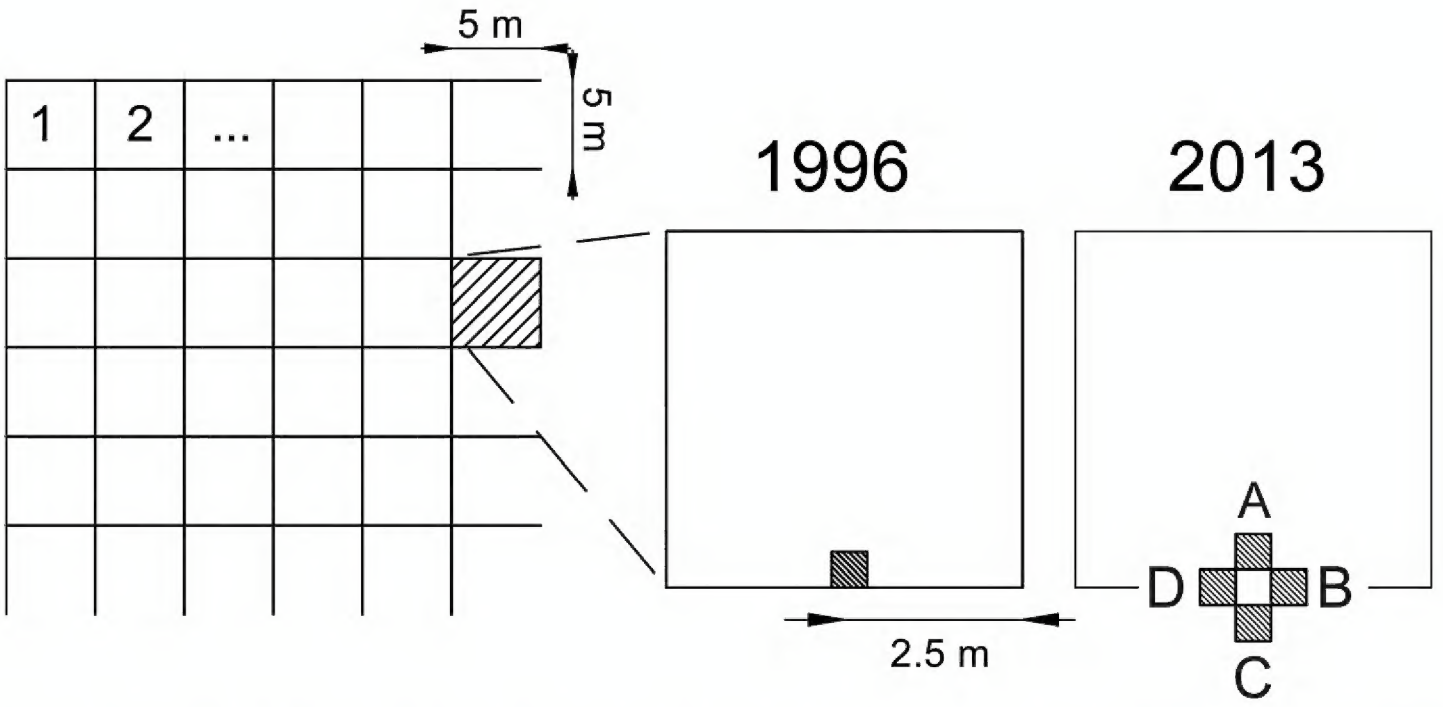

Figure 1. Design of the sampling methods. In each cell of a 5 m × 5 m grid a 0.25 m² plot was sampled in 1996. Blocks of four 0.25 m² plots were resampled in the same grid in 2013.

tion was only possible with a 1 m accuracy. To overcome this problem we used a cluster of four 0.25 m² plots at each of the 306 points to represent the original locations (Figure 1).

The five stand developmental situations (SDS) were identified as follows (Table 1, Figure 2, Suppl. material 2):

Control (C): This patch was selected because the tree canopy of the closed old beech stand was undisturbed during the study period.

One-year-old gap (1YG): This gap was formed in 2012 by the fall of two large beech trees.

Three-year-old gap (3YG): This gap was created by the fall of five trees in spring 2010.

Old beech gap (OBG): This gap was formed by the fall of a single large beech tree in the early 1990s.

Old collapse (OCO): It was opened in the early 1980s.

The 306 plots resurveyed in 2013 were selected to include both the centres and the peripheries of the five SDSs (see Suppl. material 1). The results are presented for three different spatial scales as follows (Table 2):

Stand-scale: Data from all the 306 plots are lumped together to characterise the 1 ha patch.

Stand developmental situation (SDS) scale: Each SDS is represented by the joined data of 25 plots located in the centre of an individual SDS. Thus, an approximately 400 m² area is sampled (which is comparable to the size of standard phytosociological relevé) for each SDS.

Table 1. Summary information on the five stand developmental situations (SDS) studied. For explanations of the stand developmental situations, see methods.

SDS	Soil depth	Canopy in 1996	Canopy in 2013	Herb layer in 1996	Herb layer in 2013
C	shallow	closed	closed	sparse	unchanged
1YG	shallow	closed	open	sparse	increased
3YG	shallow	closed	open	sparse	increased
OBG	deep	open	closed	dense	decreased
OCO	rocky	open	closed	dense	decreased

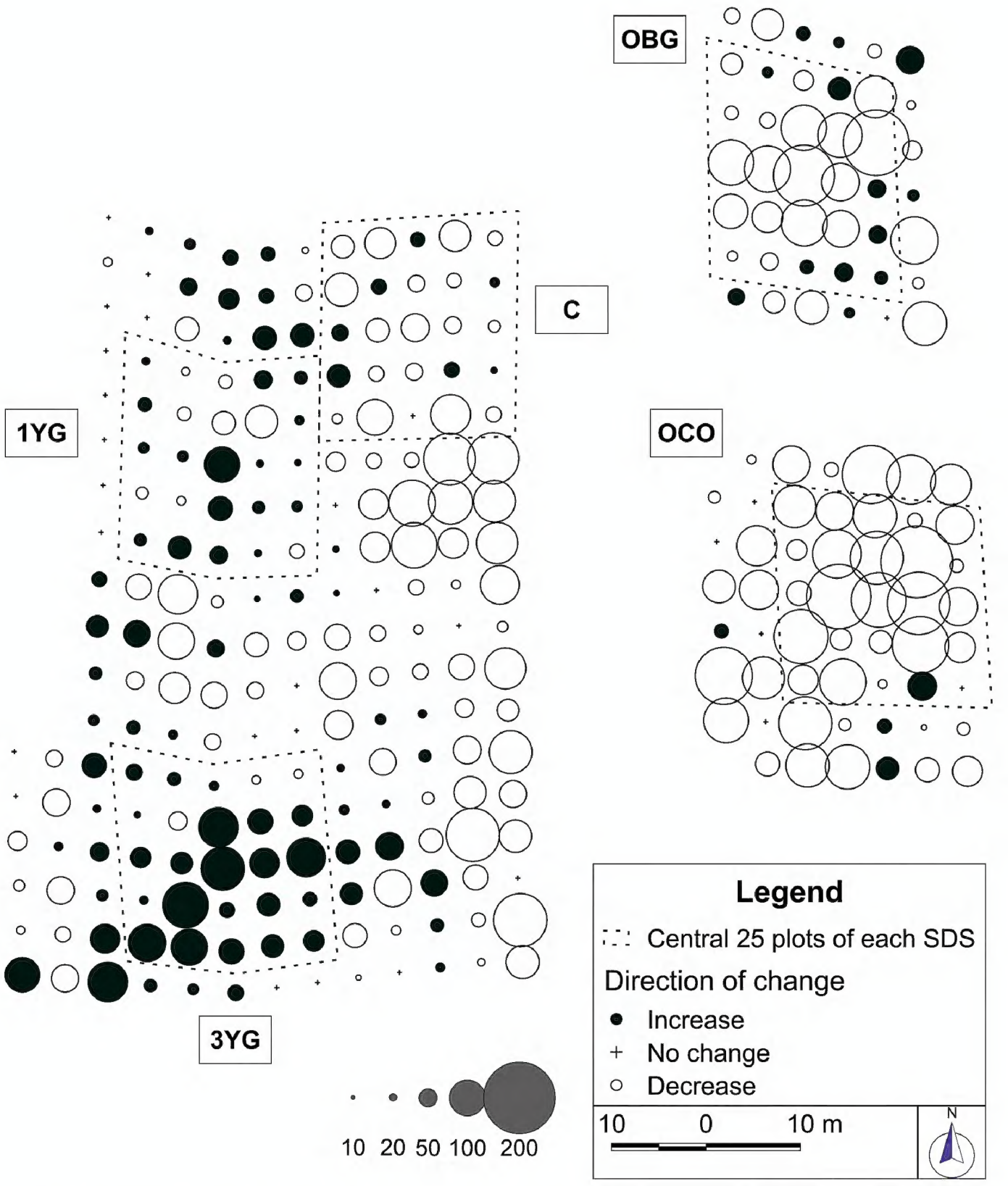

Figure 2. Changes in total herbaceous-layer vegetation cover (%) between 1996 and 2013. Dotted lines indicate the borders of the samples representing the five stand developmental situations (C, 1YG, 3YG, OBG, OCO).

Table 2. Summary information on spatial scales and number of sampling units used in this study (SDS = stand developmental situation).

Scale of study	Represented area	Number of plots	
		In 1996	In 2013
Stand	1 ha	306	306×4 = 1224
SDS	400 m²	5 SDS×25 = 125	5 SDS×25×4 = 500
Local	0.25 m²	306	306×4 = 1224

Fine-scale: All the 306 plots are treated separately so changes at the 0.25 m² scale can be described. Table 2 summarises the scales and numbers of sampling units in this study.

Data analyses

For our analyses we used the following variables:

Cover of the herbaceous layer: For each plot we used the sum of estimated cover values of individual species, so > 100% values can occur. Mean cover and maximal cover were calculated from the plot data for the whole stand and for the five SDSs. For the 2013 data the overall means were used: 1224 plots (306×4) for the stand-scale, 500 plots (4×125) for the SDS-scale. Changes in the abundance of herbaceous vegetation were calculated as change in total cover. To get a better understanding of the dynamics of individual species at the stand- and SDS-scales, both net and absolute cover change were calculated.

Species richness of the herbaceous layer: The number of species was calculated for all the three spatial scales and for the two sample years. The average species number per plot was also compared.

To quantify changes that occurred during the 17 years we used the mean values of the four subsamples of 2013 data (mean species richness, mean cover of the herbaceous layer of each plot). In this way we used an equal number of plots as in 1996 for the comparisons (306 plots for stand- and fine-scale, and 125 plots for SDS-scale analyses). The relationships between stand developmental situations (SDS) and magnitude of change in species richness and total herbaceous cover were studied by using Kruskal-Wallis test (H statistics), the non-parametric analogue of classical analysis of variance (Conover 1980). Wilcoxon matched pairs test was used to test the differences between the two surveys regarding temporal changes of species richness and total herbaceous cover at SDS- and fine-scale.

In order to quantify the changes in a species pool the following variables were calculated, where in the case of 2013 data the average values of the four subsamples were used for all calculations:

Number of colonisation events: Individual colonisation events were detected at the fine-scale (0.25 m²). The number of colonisation events (appearance of a species) was

expressed as sum (all new occurrences of all species) and mean (average number of new occurrences per plot) for each spatial scale studied.

Number of extinction events: Individual extinction events were detected at the fine-scale (0.25 m^2). The number of extinction events (disappearance of a species) was expressed as sum (all disappearances of all species) and mean for each spatial scale studied.

Absolute species turnover in the herbaceous layer: Absolute turnover in species composition between successive sampling years was calculated as (E + C)/2, where E and C are the number of species extinctions and colonisations, respectively (Williamson 1978).

Relative species turnover in the herbaceous layer: Relative turnover was calculated as (E + C)/(S1 + S2) × 100%, where E and C are as above and S1 and S2 are the number of recorded species present in the two years (Diamond 1969).

Colonization and extinction events and the species turnover in the herbaceous layer were also assessed in a qualitative way. The behaviour of individual species was analysed at the stand- and SDS-scales.

When the effect of relocation was analysed, we compared the size of time effect (i.e. the difference between the 1996 value and the average value of the four 2013 subsamples) and the size of relocation effect (i.e. average of paired differences between the four subsamples) by Wilcoxon matched pair test. A one-sided alternative hypothesis was applied, i.e. higher time than relocation effect. Significant differences imply that the observed differences between two sampling times cannot be caused by the imprecise re-allocation of the subsamples only.

Results

Cover of the herbaceous layer

At the stand-scale we observed a general decrease in the abundance of herbaceous vegetation between 1996 and 2013 (Figure 2). The mean total cover/plot changed from 20.2% in 1996 to 7% in 2013.

At the SDS-scale we found profound differences in the magnitude and tendency of cover change from 1996 to 2013 (Table 3; Kruskal–Wallis test results, H = 57.31336, $p < 0.00001$). Wilcoxon matched pair test also showed significant differences between the two surveys in cover at the fine-scale (306 pairs of plots, Wilcoxon matched pair test results, T = 10863.50, Z = 6.36, $p < 0.00001$) and at SDS-scale for each SDS except for 1YG (25 pairs of plots, Wilcoxon matched pair test results, C – T = 53.00, Z = 2.771429, P = 0.005581; 1YG – T = 120.00, Z = 1.143544, p = 0.252814; 3YG – T = 17.5000, Z = 3.901502, $p < 0.0001$; OBG – T = 48.50, Z = 3.067388, p = 0.002160; OCO – T = 8.00, Z = 4.057143, $p < 0.0001$).

Vegetation cover decreased considerably in infilling old gaps (OCO: -50.3%; OBG: -30.3%), whereas it increased slightly (1YG: 1.6%) and more substantially (3YG: 16.7%) in recently created gaps.

Table 3. Total vegetation cover (%) in 1996 and 2013 in the five stand developmental situations. For explanations of the stand developmental situations, see methods.

	Mean cover in 1996 (%)	Mean cover in 2013 (%)	Max. cover in 1996 (%)	Max. cover in 2013 (%)	Max. cover change/ plot in 1996 (%)
C	14.1	5.1	56	29	-46.6
1YG	6.2	7.8	46	74	35.5
3YG	4.1	20.8	25	112	62.7
OBG	36.7	6.4	140	36	-137.4
OCO	55.0	4.7	176	75	-165.7

Table 4. Net and absolute cover change (%) of the ten most responsive species between 1996 and 2013.

Species name	Stand-scale	SDS-scale (5×25 plots)				
	306 plots	3YG	1YG	C	OBG	OCO
Net Change (%)						
Galium odoratum	-1270.80	45.00	-24.12	-123.25	-351.32	-70.00
Urtica dioica	-765.00	72.00	4.25	0.00	-25.00	-432.75
Dryopteris filix-mas	-418.55	25.00	40.75	-19.25	-147.00	-129.10
Athyrium filix-femina	-766.75	18.75	2.25	0.00	16.25	-429.25
Mercurialis perennis	-375.25	12.25	2.00	-9.87	-56.62	0.00
Fagus sylvatica	-115.95	40.50	0.90	5.00	-121.25	0.00
Geranium robertianum	-279.35	0.75	-24.50	-2.00	-5.10	-24.50
Cardamine bulbifera	34.50	0.00	11.75	-29.50	20.72	0.50
Solanum dulcamara	108.00	41.50	8.75	0.00	0.00	-15.00
Acer pseudoplatanus	105.87	80.12	0.37	1.75	3.42	-1.00
Absolute change (%)						
Galium odoratum	1646.35	90.00	72.37	131.75	353.37	70.00
Urtica dioica	948.50	72.00	4.25	0	25.00	432.75
Dryopteris filix-mas	899.35	25.00	49.75	22.75	173.00	142.10
Athyrium filix-femina	885.75	18.75	2.25	0.00	16.25	436.75
Mercurialis perennis	640.75	71.25	36.00	54.37	80.37	0.00
Fagus sylvatica	364.95	40.50	9.10	15.00	147.25	0.00
Geranium robertianum	310.85	6.75	25.50	6.00	5.10	73.00
Cardamine bulbifera	263.95	0.00	11.75	77.50	36.17	0.50
Solanum dulcamara	236.50	41.50	8.75	0.00	0.00	21.00
Acer pseudoplatanus	235.47	82.12	12.37	12.25	7.62	1.00

At the fine-scale, i.e. at the scale of individual plots, the largest decrease and increase in total cover was -165.7% and 62.7% respectively.

The observed changes in mean cover were obtained as the balance of positive and negative changes in individual species. Most changes were attributed to only a few species. As Table 4 shows, the sum of absolute cover changes was the highest for *Galium odoratum*, followed by *Urtica dioica* and the two fern species. A large difference between absolute and net change within an SDS indicates intensive fine-scale dynam-

ics (increase and decrease in cover occur simultaneously in individual plots belonging to an SDS). This behaviour is characteristic of forest specialist species such as *Galium odoratum* (3YG, 1YG), *Cardamine bulbifera* (C, OBG) and *Mercurialis perennis* (3YG, 1YG, C, OBG)

Species richness of the herbaceous layer

In 1996 and 2013 we recorded 42 and 48 species, respectively, though in the latter case a four times larger area was sampled because of the four subsamples used (306 plots×4). At the stand-scale our full sample (306 locations, two surveys) contained data from 54 species (45 herbs, 6 trees, 3 shrubs), of which 50 species occurred in the 125 plots representing the five SDSs.

In contrast to the relative stability in species richness at the stand-scale, a much more variable picture was obtained when the SDS-scale was studied. In 1996 species richness varied between 7 and 23 (Table 5) in the five SDSs (25 plots each), whereas the same number were in the range of 14–31 in 2013. As Table 5 and Figure 3 show, the largest change in SDS-scale species richness took place in the three-year-old gap (3YG), where it grew from 7 to 31. Species richness was the most stable in the control, where it changed from 15 to 14. When mean species richness/plot was considered, the largest change was found in OCO, where it decreased to almost one-tenth of the original 3.7 in 1996.

We found significant differences between the five SDSs in changes in species richness from 1996 to 2013 (Kruskal–Wallis test results, $H = 56.1961$, $p < 0.00001$). At the fine-scale (individual 0.25 m^2 plots) species richness was in the range of 0-10 and 0-8 in 1996 and in 2013, respectively, with high variation among the five SDSs (Table 5). Significant differences were also found between the two surveys for each SDS (25 pairs of plots, Wilcoxon matched pair test results, C – T = 47.00, Z = 2.942857, p = 0.003252; 1YG – T = 8.00, Z = 3.84718, p = 0.00012; 3YG – T = 21.00, Z = 3.807328, p = 0.000141; OBG – T = 17.00, Z = 3.680209, p = 0.000233; OCO – T = 0.00, Z = 4.285714, p = 0.00018), as well as at the fine-scale (306 pairs of plots, Wilcoxon matched pair test results, T = 9443.500, Z = 7.023608, p < 0.00001).

Table 5. Species richness in 1996 and 2013 in the five stand developmental situations (SDS). For explanations of the stand developmental situations, see methods. SpNo = species number.

SDS	Species richness in 1996	Species richness in 2013	Mean SpNo/plot in 1996	Mean SpNo/plot in 2013
C	15	14	2.44	1.27
1YG	12	24	1.12	1.48
3YG	7	31	0.6	2.21
OBG	23	18	4.12	1.53
OCO	19	15	3.68	0.4

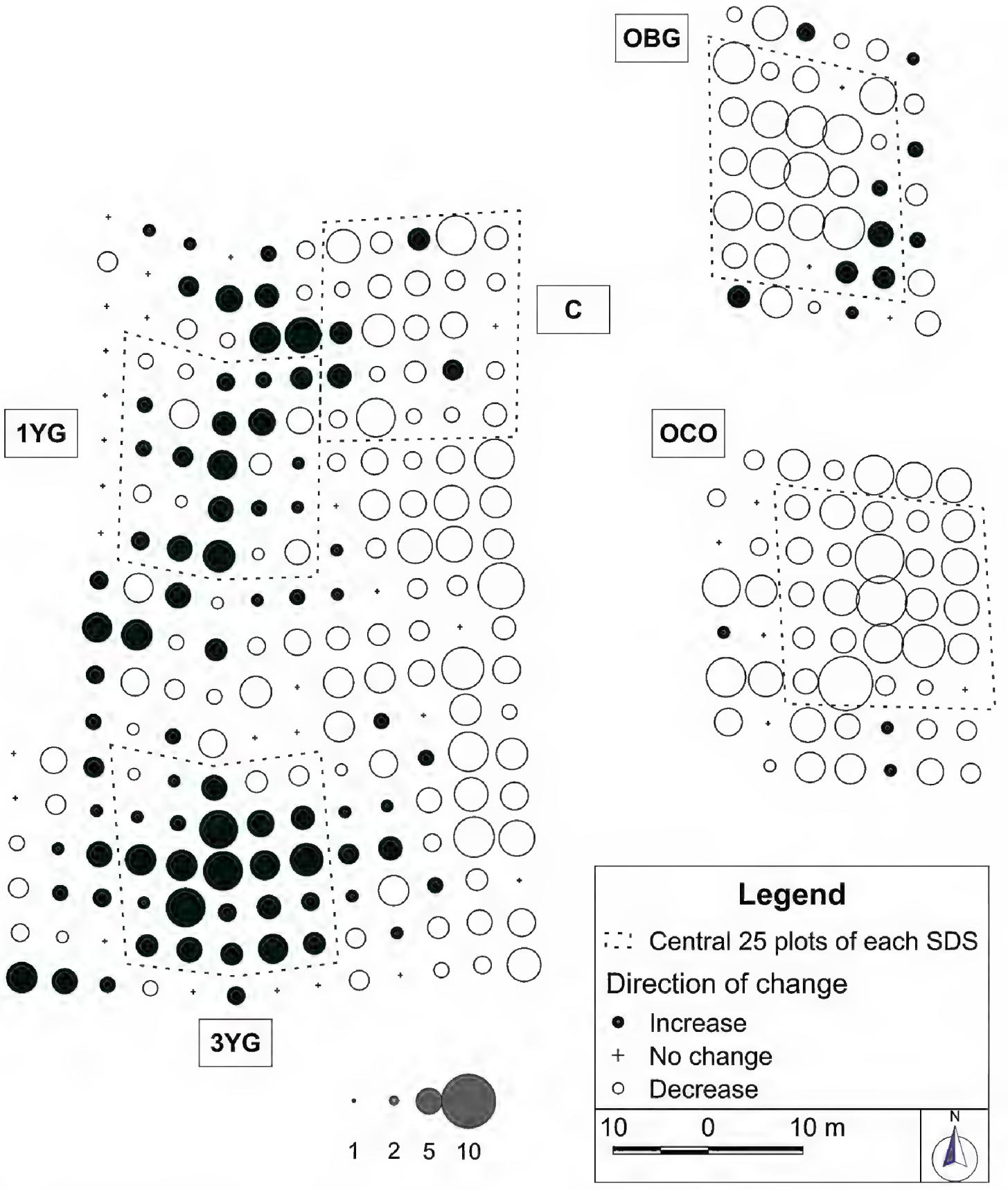

Figure 3. Changes in species richness between 1996 and 2013. Dotted lines indicate the borders of the samples representing the five stand dynamic situations (C, 1YG, 3YG, OBG, OCO).

Number of extinction and colonization events and species turnover in the herbaceous layer

Quantitative

Species extinctions and colonisation occurred at all spatial scales studied during the 17 years between the two samplings. At the stand-scale there were only six species that dis-

Table 6. Number of extinction and colonisation events (overall mean of the four subsamples at each plot), absolute and relative species turnover in the five stand developmental situations (SDS) based on resurvey data collected in 1996 and 2013. For explanations of the stand developmental situations, see methods.

SDS	Extinction	Colonisation	Mean Absolute Turnover/Plot	Mean Relative turnover (%)
C	77.25	20.5	1.95	117.11
1YG	43	30.25	1.46	121.07
3YG	19.75	48.25	1.36	105.26
OBG	109.75	16.25	2.52	99.53
OCO	127.5	5.75	2.66	137.25

appeared, but all of them were present at very low frequencies and abundances in 1996. Half of the recorded 12 newly occurring species were actually present in the 576 plots sampled in 1996, but were not included in the sample (306 plots) used for the resurvey.

At the SDS-scale there were considerable differences among the individual SDS. As Table 6 shows, the number of extinctions was the highest in OCO and OBG, whereas – as was expected – colonisation was the most intensive in 3YG. Mean absolute turnover was the highest in OCO and OBG, mostly because of the high number of extinctions. If we also consider the size of the species pool, relative turnover was the highest in OCO, followed by 1YG, where the initial species richness was very low. Fine-scale (0.25 m^2) colonisation was in the range of 0 and 4.75 in the 306 plots, with a mean value of 0.717. The same values for extinctions were 0, 10 and 1.4, respectively.

Qualitative

Quantitative results indicate relative stability at the stand-scale and rather intensive dynamics at the SDS- and fine-scales. However, to get a better understanding of the processes, it is worth looking at what species become extinct or colonise in different situations. Special interest is devoted to closed forest specialist species (Schmidt et al. 2011), which are marked in bold in the text below.

At the stand-scale, the six species that were not included in the 2013 sample were all forest species (***Chrysosplenium alternifolium***, *Epilobium montanum*, ***Hordelymus europaeus***, ***Melica uniflora***, ***Monotropa hypopitys***, *Viola odorata*) that occurred at very low abundances in 1996. Half of the newly colonising 12 species were forest species (***Actaea spicata***, *Campanula rapunculoides*, ***Epipactis helleborine***, *Hieracium acuminatum*, *Poa nemoralis* and ***Polygonatum verticillatum***) that were recorded as new because of similar chance effects since, according to our field records, they were all present in 1996 within the studied 1.5 ha stand. Among the colonisers there were two ruderal species (*Tussilago farfara*, *Cirsium arvense*) and one newly appearing adventive species (*Impatiens parviflora*).

At the SDS-scale it is worth comparing the list of disappearing and newly appearing species. In the OBG, most extinctions were of closed forest species (e.g. ***Galium odoratum***,

Table 7. Closed forest specialist species that disappeared from individual SDS (based on data of 25 plots each) by 2013. Numbers in brackets indicate the original number of occurrence of the species in 1996. For explanations of the stand developmental situations, see methods.

	Closed forest specialist herbaceous species	
SDS	**Disappearing**	**Surviving**
C	*Melica uniflora* (1)	*Cardamine bulbifera, Dryopteris filix-mas, Euphorbia amygdaloides, Galium odoratum, Mercurialis perennis, Viola reichenbachiana*
1YG	none	*Dryopteris filix-mas, Galium odoratum, Galium odoratum, Viola reichenbachiana*
3YG	none	*Galium odoratum, Mercurialis perennis,*
OBG	*Circaea lutetiana* (1); *Hordelymus europaeus* (1); *Moehringia trinervia* (1); *Oxalis acetosella* (2); *Pulmonaria obscura* (1)	*Cardamine bulbifera, Dryopteris filix-mas, Euphorbia amygdaloides, Galium odoratum, Mercurialis perennis, Viola reichenbachiana*
OCO	*Chrysosplenium alternifolium* (1); *Galium odoratum* (2)	*Dryopteris filix-mas, Lamiastrum galeobdolon luteum, Impatiens noli-tangere, Oxalis acetosella, Polystichum braunii*

Mercurialis perennis, ***Viola reichenbachiana***, ***Cardamine bulbifera***) and there were only a few extinctions of gap or disturbance indicating species (*Chelidonium majus*, *Geranium robertianum*, *Rubus idaeus*, *Urtica dioica*). Colonisation events were almost exclusively due to closed forest specialist species. At the rocky OCO site the observed extinctions were mainly attributable to those species (e.g. ***Dryopteris filix-mas***, ***Impatiens nolitangere***, *Solanum dulcamara*, *Urtica, dioica*) that occurred with high frequencies in 1996. The low number of colonisation was due to similar species because site conditions are not favourable for most closed forest specialist herbs. On the contrary, in the control plot the species pool did not change much, despite the relatively intensive dynamics (77 extinctions, 20 colonisations). Extinctions and colonisations were both due to real closed forest specialist herbs (e.g. ***Cardamine bulbifera***, ***Euphorbia amygdaloides***, ***Galium odoratum***, ***Mercurialis perennis***). In 3YG and 1YG only a low number of extinctions were recorded, mostly due to the disappearance of forest species. The large number of colonisations in these gaps was attributable to both typical gap species and to those forest species that are able to react relatively fast to changing light conditions.

Table 7 shows how successfully closed forest species (Schmidt et al. 2011) survived in the individual SDS. Only a few species with low original frequencies disappeared, indicating the overall successful survival of this species group.

Effect of relocation error

Our results on the effects of relocation error showed that time effect was significantly higher than relocation effect both in the case of species richness (306 pairs of plots, Wilcoxon matched pair test results, $T = 8475$, $Z = 7.769055$, $p < 0.00001$) and in the case of total cover of the herbaceous layer (306 pairs of plots, Wilcoxon matched pair

test results, T = 9932, Z = 6.983762, p < 0.00001). Consequently, differences between data from 1996 and average data of the four subsamples of 2013 cannot be merely attributable to imprecise relocation of subsamples.

Discussion

After 17 years we found low species turnover and a general decrease in herbaceous cover at the stand-scale. Therefore, our first hypothesis is only partly supported. We found an overall stability of the species pool in the herbaceous layer at the stand-scale, whereas the abundance of vegetation (measured as total herb cover) changed considerably.

Several analyses pointed out that a decrease in herbaceous cover in a temperate forest is attributed to light deficit caused by a denser canopy. This can be a consequence of less intensive forest management or even abandonment, as well as the lack of natural disturbance including the activities of grazers (Brewer 1980, Davison and Forman 1982, Vera 2000, Verheyen et al. 2012, Kopecky et al. 2013). A drastic decrease in herbaceous species cover was found by Łysik (2008) in a primeval beech forest in Poland and by Ujházy et al. (2007) in a primeval fir-beech forest in Slovakia. Both studies connected this sharp decrease with the massive recruitment of woody regeneration. The observed decrease in our case can also be related to the partial closure of the canopy, and to the infilling of the two main former canopy gaps with young woody species (see below). The majority of the reduction in the herb cover was due to a few forest species (***Galium odoratum***, ***Mercurialis perennis***) and to species (*Urtica dioica*, ***Dryopteris filix-mas***, ***Athyrium filix-femina***) that were abundant in gaps in 1996. Hence, we argue that stability of herbaceous cover might be realized on a larger study site, where all stand dynamic situations are represented in natural proportions. We also assume that the extremely dry years of 2012 and 2013 as a potential climate factor could have contributed to the observed decrease.

The majority of the temperate forest resurvey studies document high species turnover, as a consequence of environmental change. Denser canopies effect not only the cover of the herbaceous layer, but also trigger trait-based reactions as the decrease in light-demanding species and increase in species with good abilities for living in shade (Brewer 1980, Hédl et al. 2010, Heinrichs et al. 2014). A direct trend in species trait shift can be observed in spite of the formerly assumed or postulated stability of a site (Brewer 1980, Taverna et al. 2005, Łysik 2008). Despite the expected stability, results of Taverna et al. (2005), for example, showed systematic changes in herbaceous species richness in a climax hardwood forest in North-Carolina, as a potential result of the elimination of ground fires and widespread grazing typical at the beginning of the twentieth century. Invasive species can significantly change the composition of the herbaceous layer even in primeval forests (Łysik 2008). One of the few examples, where the ground vegetation showed an overall stability, is reported from a Danish beech forest by Carøe et al. (2000), but the temporal scale was very short (5 years). Similar stability of species pool was found by Woods et al. (2012) in unmanaged northern

hardwood forests over a three-decade period. These results highlight the rarity of the observed low species turnover of Kékes Forest Reserve after almost two decades, where all extinct species were represented with very low abundances in 1996; similarly, all colonization happened with low abundance and many of the colonizing species were present in the species pool of the close surroundings.

Our results support the concept that the experienced intensive fine-scale dynamics is profoundly governed by the stand dynamic events of the studied forest stand. Significant differences were found between the individual SDSs and between years in herbaceous cover, species richness and species turnover at the SDS-scale. Highest species richness, mean species number/plot and highest herb cover characterized the two main gaps (OCO and OBG) in 1996. An expressed decrease in the herbaceous layer cover was observed after 17 years in these two, gradually closing gaps, where the saplings have overgrown and started to cast shadow on the herbaceous plants. Lateral canopy expansion of bordering trees has also contributed to gap closure. A very high number of extinctions with high absolute species turnover were detected in these situations. In the old collapse (OCO) the cover of ***Dryopteris filix-mas***, ***Athyrium filix-femina***, and *Urtica dioica* was drastically reduced. In the old beech gap (OBG) pronounced recession of ***Galium odoratum***, ***Dryopteris filix-mas***, ***Fagus sylvatica*** (young beech individuals have grown out of the herbaceous layer) and ***Mercurialis perennis*** was detected. Competition between the herbaceous plants and the saplings, especially with the very competitive beech saplings, and the resulting drop in herbaceous plant cover, was observed by several authors (Davis et al. 1998, Łysik 2008, Ujházy et al. 2007, 2013). On the other hand, the two younger gaps, created in 2010 and 2012 (3YG, 1YG) had low species richness, low mean species/plot and low herbaceous cover at the beginning, as the canopy was closed in 1996. The resurvey detected a sharp increase in both species richness and cover in the case of the three-year-old gap (3YG), where the massive colonization process was performed by gap specialists (*Urtica dioica*, *Solanum dulcamara*), by responsive forest species (***Dryopteris filix-mas***, ***Galium odoratum***) and by tree seedlings (***Fagus sylvatica***, *Acer pseudoplatanus*). All these changes were more moderate in the case of 1YG, due to the shorter time-span. Despite the high absolute species turnover, the cover of the herbaceous layer and species richness changed only slightly in the control SDS. These results support our second hypothesis that stand dynamic events govern the herb cover, and drive the herbaceous layer changes, at least during this nearly two decades in our study site.

The Slovakian fir-beech forest investigated by Ujházy et al. (2005, 2007) had a very similar species pool in the herbaceous layer as our studied site. They found relatively low species turnover – compared to commercial forests – in the three developmental stages; rather the abundance or dominance values differentiated the growing, optimum and decay stages (Ujházy et al. 2005). The investigated short-term (4 year) changes were attributable to stand dynamics; they recorded a rapid change in the herb layer during the four-year period established in young gaps (Ujházy et al. 2007). However, they did not analyse colonisation and extinction patterns for all species.

Although the four subsamples of each plot were relocated only with a 1 m accuracy in 2013, statistical tests proved that the time effect (change in vegetation) was significantly higher than the relocation effect. With this we managed to assure that the interpreted temporal changes were not artefacts resulting from imperfect relocation.

Conclusion

We found that intensive local-scale extinction and colonization episodes were balanced at the stand-scale, resulting in overall stability of the species pool in the herbaceous layer vegetation. These results have important implications for both forest management and conservation.

The observed stand dynamics driven changes of vegetation indicate that the use of small regeneration areas in forest management can prevent competitive ruderal species (e.g. *Calamagrostis epigejos*) from causing serious problems in regeneration (Gálhidy et al. 2006, Kelemen et al. 2012).

From a conservation viewpoint, one of the most important species-related implications is that the long-term survival of closed forest specialists, including ancient forest indicators (Peterken and Game 1984, Hermy et al. 1999), could be guaranteed by management techniques mimicking natural small gap dynamics. This is important for several of those species that are seriously dispersal limited, meaning that once they disappear it is extremely hard, or it takes decades to centuries, to recolonize secondary forests (Kelemen et al. 2014). We assume that the observed stability in the species pool was secured by the primeval character of Kékes Forest Reserve. By primeval we refer to both structurally rich old-growth character and long forest continuity. The former is illustrated by the presence of all important forest developmental phases produced by natural stand dynamics (natman report 2002) and the high amount and diversity (size and decay phase) of deadwood (Christensen et al. 2005) and also of forest specialist organisms (e.g. Ódor 2000, Ódor and Standovár 2001, Ódor et al. 2006, Standovár et al. 2006, Heilmann-Clausen et al. 2014). Long continuity is convincingly documented by Czájlik (2009). Similar relationships between the richness in ancient forest indicator plants and that of other organism groups were shown, for example, by Hofmeister et al. (2014) for macrofungi.

Several studies documented that habitat specialist species occur in the highest numbers in forested landscapes with long continuity of forest structures and habitats (for a review see e.g. Nordén et al. 2014). This emphasizes the specific conservation role of even small remnants of virgin or ancient forest, as they secure the long-term survival of habitat specialists, and they might also serve as a source for dispersal from these remnants into the surrounding landscape.

In areas, where nature conservation is not the sole purpose of management, managers have started to apply retention forestry as a means of integrating conservation concerns into forest management. A thorough review (Fedrowitz et al. 2014) showed that retention cuts supported greater abundance and higher species richness of forest species than clear-cuts. This positive effect increases with the proportion of retained

trees and time since harvest. However, they also showed that retention cuts cannot be a substitute for uncut forest because it had negative impacts on mostly closed forest specialist species.

All these suggest that for successful conservation of forest biodiversity we still need to preserve existing remnants of woodlands with high conservation value and also to apply a mix of management approaches in their immediate surrounding that support natural processes and the creation of important habitats.

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Supplementary material 1

Map showing the position of sampling plots in 1996 and 2013
Authors: Tibor Standovár, Soma Horváth, Réka Aszalós
Data type: specimens data
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Supplementary material 2

Map showing canopy trees in the study area.
Authors: Tibor Standovár, Soma Horváth, Réka Aszalós
Data type: specimens data
Copyright notice: This dataset is made available under the Open Database License (http://opendatacommons.org/licenses/odbl/1.0/). The Open Database License (ODbL) is a license agreement intended to allow users to freely share, modify, and use this Dataset while maintaining this same freedom for others, provided that the original source and author(s) are credited.